SHORT COMMUNICATION

Snatching prey from the mandibles of ants, a feeding tactic adopted by East African jumping spiders

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Abstract. Instances are documented of salticids robbing ants by adopting a specialized behavior pattern, "snatching." The salticid positioned itself beside an ant column on the wall of a building, repeatedly fixating its gaze on different individual ants in the column and maintaining fixation on the ant by turning its body while the ant walked by. When close to an ant that was carrying prey, the salticid maneuvered about so that it was head on, grabbed hold of the prey using its chelicerae, and then rapidly pulled the prey out of the ant's mandibles. Having secured the prey, the salticid moved away from the ant column to feed. All observations were made at Mbita Point, by the shore of Lake Victoria in western Kenya. The salticids were three species of *Menemerus* (Simon 1868): *M. bivittatus* (Dufour 1831), *M. congoensis* Lessert 1927 and an undescribed species, *Menemerus* sp. n. The ant species were from the genera *Crematogaster* (Lund 1831) and *Camponotus* (Mayr 1861). In all instances, the salticid was 2–6 mm in body length (juveniles of all three *Menemerus* species and adults of *Menemerus* sp. n). Prey items taken from ants were, in most instances, "lake flies" (adults of Chaoboridae and Chironomidae).

Keywords: Salticidae, ants, predation, stealing prey, Chironomidae, Chaoboridae

In the tropics, ants (Formicidae) are the dominant insects (Hölldobler & Wilson 1990) and jumping spiders (Salticidae) are the dominant spiders (Coddington & Levi 1991), but we are only beginning to understand how salticids and ants interact (Nelson & Jackson 2005, 2006a,b; Nelson et al. 2006). Salticids are unique among spiders because of their complex eyes (Land 1969; Blest et al. 1990), exceptionally acute vision (Land & Nilsson 2002) and intricate vision-guided predatory behavior (Jackson & Pollard 1996; Harland & Jackson 2004). Most species in this large family (about 5,000 described speeies, Platnick 2008) appear to be active hunters that prey primarily on a variety of insects, but typically they do not prey on ants. It may not be surprising that many salticid species can detect ants by sight and then avoid coming close to them (Nelson & Jackson 2006c), particularly considering the formidable defences shown by ants (Blum 1981; Hölldobler & Wilson 1990), including powerful mandibles, poison-injecting stings and formic-acid sprays, and the fact that ants are sometimes predators of salticids (Nelson et al. 2004).

Yet there is a large minority of saltieids (the "myrmecophagic species") that selects ants as preferred prey (Li & Jackson 1996; Clark et al. 2000; Jackson & Li 2001; Huseynov et al. 2005) and one salticid species, Cosmophasis bitaeniata (Keyserling 1882), is known to combine chemical ant mimicry with myrmecophagy (Allan & Elgar 2001) (i.e., by mimicking the cuticular hydrocarbons of the Australian weaver ant, Oecophylla smaragdina (Fabricius 1775), C. bitaeniata gains entry to the weaver ant's nest and feeds unmolested on the ant's larvae). Here we revisit a different style of exploiting ants - robbing ants of objects they carry in their mandibles. This was first described by Bhattacharya (1936) who observed juveniles of Menemerus bivattatus (Dufour 1831) (formerly Marpissa melanognathus) in India grabbing food out of the mandibles of fire ants, Solenopsis geminata (Fabricius 1804). Our own observations show that this tactic, which we will call "snatching from ants" or just "snatching," for short, is unique neither to India nor to *M. bivittatus*. The baseline information we provide here is a step toward later quantitative and experimental research concerned with this poorly understood foraging method.

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METHODS

Menemerus is a large, well-defined genus, probably with many of the African species yet to be described (Wesolowska 1999). Our observations were on *M. bivittatus* (Dufour 1831), M. *congoensis* (Lessert 1927) and a new, undescribed species, *Menemerus* sp. n. all three of which are common in East Africa (see Jackson 1986, 1999). Typical body lengths of adult females of each species are: *M. bivittatus*, 10 mm; *M. congoensis*, 7 mm; *Menemerus* sp. n. 5 mm. Voucher specimens of all species from this study (salticids, ants, and prey) have been deposited with the Florida State Collection of Arthropods in Gainesville and the National Museums of Kenya in Nairobi.

Our study site was by the shore of Lake Victoria in western Kenya (Mbita Point, the Thomas Odhiambo Campus of the International Centre for Insect Physiology and Ecology). Mbita Point is 1200 m above sea level ($0^{\circ}25'S-0^{\circ}30'S$, $34^{\circ}10'E-35^{\circ}15'E$) and has a mean annual temperature of 27° C. In this habitat, midges (Diptera: Chironomidae & Chaoboridae), known locally as "lake flies," are exceedingly abundant (Beadle 1981), often covering the walls of buildings. As midges have notoriously short life spans, lake-fly swarms quickly turn into enormous numbers of lake-fly corpses which are routinely scavenged by ants.

We opportunistically observed *Menemerus* and other salticids when they were seen in the vicinity of ants on building walls. Whenever we saw a salticid persistently orienting toward an ant (identified to genus only), we continued observation for 30–60 min or until the salticid secured the prey. First we made about 30 preliminary observations of *Menemerus* sp. n. snatching lake flies from an unidentified species of *Crematogaster* (Lund 1831), but with no attempt made to identify the lake fly to family and no records kept concerning the salticid other than the species to which it belonged. We videotaped 10 of these preliminary observations for more detailed information about behavior.

This was followed by observations (n = 98) that were more standardized with respect to the information we recorded. After each of these observations, we collected the salticid, the ant and the "prey" (i.e., object snatched from an ant). Salticids were identified to species,

ants to genus and lake flies to family. We also recorded whether the salticid was a juvenile or an adult, and we recorded whether adults were male or female. Earlier convention (Jackson and Li 2001) is adopted for indicating frequencies of occurrence: "usually," "often," "typically," and "typical" indicate ca 80% or more.

RESULTS

Snatching from ants.—The three *Menemerus* species, as well as *Evarcha culicivora* (Wesolowska & Jackson 2003), *Harmochirus brachiatus* (Thorell 1877), *Hosarius adansoni* (Audouin 1826) and unidentified species of *Hyllns* (Koch 1846), *Natta* (Karsch 1879), *Myrmarachne* (MacLeay 1839), *Plexippus* (C.L. Koch 1846), and *Thyene* (Simon 1885), were common on the walls of buildings, with many other salticids present in smaller numbers. However, only the three *Menemerus* species were observed snatching from ants.

In the records of salticids snatching from ants (n = 98), salticid body length varied from 2 mm (n = 1, 1%, Menemerus sp. n.) to 6 mm (n = 1, 1%, M. bivittatus), with 6 (6%) being 3 mm, 27 (28%) being 4 mm and the majority (n = 63, 64%) being 5 mm. For the majority records of snatching from ants (n = 98), the salticid was *Menemerus* sp. n. (78, 80%), with 58 (74%) of these 78 records coming from adult females, 6 (8%) coming from adult males, and 14 (18%) coming from juveniles. For all records for *Menemerus congoensis* (n =10, 10% of 98) and *M. bivittatus* (n = 10, 10%), the salticid was a juvenile. The ants were undetermined species from the genus *Crematogaster* (n = 72, 73%) and *Camponotus* (Mayr 1861) (n =26, 27%).

Observed snatching sequences took place either in the morning (07:00-11:00 hours, n = 75) or in the late afternoon (17:00-11:00 hours, n = 75)19:00 hours, n = 23). The objects snatched from ants were usually (90, 92% of 98) dead lake flies (body lengths: 5 to 10 mm) (chironomid, n = 77, 79% of 98) and chaoborid (n = 13, 13%). Besides lake flies, adult females of Menemerus sp. n. (body length 5 mm) were also observed snatching an ant egg (n = 1), a dead mayfly (Ephemeroptera, n = 1), a dead *Crematogaster* worker (n = 3) and what appeared to be plant material (n = 3), with all of these objects being comparable to lake flies in size. Menemerus sp. n subsequently ate the mayfly and the ant egg, but released and moved away from the plant material and the dead ant a few seconds after contact. There were also five instances in which Menemerus sp. n. (3 adult females and 2 juveniles) snatched a dead lake fly (not identified to family) from an ant and then, a few seconds later, released the lake fly and walked away. In all other instances, the salticid ate the lake fly it snatched from an ant.

Behavioral sequences were similar irrespective of the different prey, ant genus, *Menemerus* species and, for *Menemerus* sp. n., whether the salticid was a juvenile, an adult male, or an adult female. Five behavioral stages were discerned: tracking, intercepting, attacking, retreating, and feeding.

Tracking: a salticid positioned itself beside an ant column on the wall of a building, repeatedly fixating (i.e., aligning the gaze of the corneal lenses of its anterior-medial eyes) on different individual ants active in the column and maintaining fixation on each ant for 5 s or longer by continually turning its body while the ant walked by. The ant being tracked was usually carrying an object in its mandibles. The salticid usually remained 50-100 mm from the ant while tracking and stepped out of the way whenever an ant turned and moved in its direction.

Intercepting: a spider that had been tracking suddenly began stepping about and maneuvering into position in front of the ant, effectively blocking the ant's forward progress. This usually happened only a few seconds after the salticid was first seen tracking, as any longer delay usually resulted in the ant moving far away from the salticid. When intercepting, *Menemerus* usually took a veering path and approached the ant column 20–45° off from straight ahead of the targeted ant's forward trajectory. When *Menemerus* stepped in front of the ant, the ant either stopped momentarily before moving off in a different direction or it just slowed down and veered to the side, with *Menemerus* continuing to maneuver itself in front of the active ant.

Attacking: during one of an ant's momentary pauses when being intercepted or else while the ant was attempting to step out of the way, a spider suddenly extended its rear legs, moved its body 1–2 mm forward, brought its chelicerae into contact with an object in the ant's mandibles and then immediately stepped a few millimeters backwards or to the side, pulling the object out of the ant's mandibles. In all instances, the ant released the object when the salticid pulled away.

Retreating: after extracting an object from the ant's mandibles, the spider turned and rapidly walked away, usually not stopping until about 100–200 mm from the ant column.

Feeding: the spider settled, usually in a space between bricks or in some other secluded location on the wall, and then proceeded to feed for 1-10 min. After feeding, the spider dropped the prey and walked away, after which it often returned to the ant column and stole another lake fly from the ants. As many as four lake flies were sometimes stolen in succession.

There were about 10 instances each for *M. congoensis* and *M. bivittatus*, and more than 40 for *Menemerus* sp. n., in which we observed a salticid briefly tracking an ant that had empty mandibles, but we never saw a salticid intercept these ants. There were also about 30 instances in which *Menemerus* sp. n. briefly tracked, but then failed to intercept, as well as 9 instances of seeing a salticid track and then intercept an ant that was carrying an object other than a lake fly, but then move away without attacking (*Menemerus* sp. n., 5 ants carrying plant material and 2 carrying a dead conspecific ant worker; *M. congoensis*, 2 carrying dead conspecifics).

DISCUSSION

Bhattacharya (1936) provided minimal descriptive detail of snatching behavior. He did not indicate how many times he observed *M. bivittatus* snatching from ants and he referred to the objects *M. bivittatus* stole as simply "food and eggs" (ant, spider, and object sizes not indicated). Yet his observations on *M. bivittatus* in India appear to have been similar to ours: tracking, intercepting, attacking (pulling the prey out of the ant's mandibles) and retreating with the prey before feeding.

Bhattacharya (1936) also observed *M. bivittatus* adults, but not juveniles, stalking, capturing, and feeding on house flies, *Musca domestica* (Linnaeus 1758) and he suggested that snatching prey from ants might be the primary foraging tactic of *M. biviattatus* juveniles. We hesitate to suggest that this is the primary tactic used by any of the active stages of any of the three *Menemerus* species we studied because we observed all stages of each of the three *Menemerus* species frequently capture and eat free (i.e., not in the mandibles of ants) living prey by practicing the stalk-and-leap routines that appear to be typical of many salticid species (Forster 1982; Richman & Jackson 1992; Jackson & Pollard 1996).

Our observations suggest instead that snatching from ants is an alternative foraging tactic sometimes adopted by small individuals (i.e., individuals no more than 6 mm in body length) of *Menemerus*. For the smallest of the three *Menemerus* species we studied (i.e., *Menemerus* sp. n.), this included adults of both sexes as well as juveniles. However, for *M. bivittatus* and *M. congoensis*, this included only juveniles.

Despite many salticid species being abundant at Mbita Point, the only salticids we saw snatching prey from ants were the three *Menenuerus* species. These observations from East Africa, together with Bhattacharya's (1936) records from India, suggest that snatching from ants may be widespread among species of *Menemerus* living in ant-rich habitats. Further work is needed for determining whether this tactic is special to the genus *Menemerus* and for clarifying the selection pressures that might have favored the evolution of snatching behavior.

It is difficult to envisage a salticid needing an ant's help overpowering inoffensive, soft-bodied lake flies and seeing building walls on the shore of Lake Victoria covered by lake flies does not suggest that finding lake flies is a pressing problem for which a salticid might need an ant's assistance. We may be tempted by an image of salticids grazing on clumps of lake flies, rather like antelopes grazing on clumps of grass, but choosing and capturing a living lake fly may be far from effortless for a salticid. Time considerations may be important. Success for *Menemerus* during stalk-leap sequences may often depends on slowly moving close enough to gauge an accurate leap, with a targeted prey potentially nullifying the salticid's efforts by flying away. Stalking sequences typically take several minutes, compared with the few seconds needed to intercept an ant.

Decision making is another potential problem for a salticid. The image of unlimited lake-fly prey changes somewhat upon close examination. Many of the lake flies covering building walls are in fact already dead, but stray silk lines left by spiders hold dead lake flies in place in lifelike postures on the wall. A light breeze often makes the dead lake flies twitch and jiggle about. *Menemerus* and other salticids were often seen stalking these dead flies, leaping on them when close and then almost immediately releasing them, but there were only five instances in which we observed *Menemerus* sp. n immediately release and move away from a dead lake fly it had snatched from an ant. Perhaps one of the primary advantages of stealing from ants is that the salticid can rely on the ant to select lake flies that are still fresh enough to be palatable.

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